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# EGG-LAYING OF CRAYFISH

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In crayfish, as in related Crustacea, the eggs are carried fastened to the limbs of the abdomen during the long period of development that precedes their hatching. As the openings of the oviducts are upon the thorax, the eggs have to be transported some distance to reach the abdominal limbs. It is the purpose of this article to describe some of the activities of the female associated with the extrusion of eggs from the oviducts, their transportation to the limbs of the abdomen, and their fixation there.

In a crayfish in France, a species of Astacus, some of the behavior of the female in laying was long since made out by Chantran (*Compt. Rend. Acad. Sci. Paris*, vol. 71, pp. 43–45, 1870; vol. 74, pp. 201–202, 1872) in his long continued and careful study of the life history of the crayfish. His too brief statements are as follows. The female crayfish stands up and for several hours secretes a viscid mucus from the limbs of the abdomen. It then lies down upon its back with the abdomen bent forward toward the openings of the oviducts, in such a way as to form a sort of chamber, in which, on the following night, the eggs were received as they were expelled from the reproductive organs. In different females the expulsion of eggs lasted from one to several hours. The eggs were plunged into the mucus which, as it were, bound the edges and the end of the abdomen to the thorax and also helped to make the boundary of the above mentioned chamber or basket. In this chamber there was some water as well as eggs and mucus. All the eggs were laid at one period and rarely were any laid in the day time.

Observations upon the laying habits of an American crayfish, *Cambarus affinis*, as published in this journal (*Amer. Nat.*, vol. 38, pp. 165–206, 1904) showed a close agreement with the above account. Renewed observations upon the same species in April, 1904, have added more details and verified suppositions previously made to bridge over gaps in observation of actual extrusion and transport of eggs.

The activities of the female connected with egg-laying may be divided, for convenience of description, into four periods. First, the preparatory cleansing of the under side of the abdomen and thorax. This lasts four or five days and has been described in the previous paper. Second, the period of secretion of mucus, or "glairing" as we may call it, to be described below. Third, the period of actual extrusion of eggs, previously inferred but described below as actually seen. Fourth, the rhythmic alternation of position of the body, or "turning," lasting several hours and described in the previous paper.

All these processes precede the long care of the eggs as they hang fastened to the abdominal legs for from five to eight weeks till they hatch, after which there is a brief period of association of female and young before the latter scatter and become independent.

The least well observed process is that of secreting glaire from the glands of the abdominal appendages and sterna. It always follows the long and very laborious cleansing of those surfaces and immediately precedes the extrusion of eggs so that as soon as the glaire is ready and the female properly posed, the eggs pass out into the glaire, one period passing insensibly into the other. At the time of secretion the female is still easily alarmed and moreover the glaire is at first seen with difficulty as it is like water in refraction, so that in most cases the "glairing" period escaped observation. But as far as was made out the secretion of the glaire took less than half an hour, though Chantran speaks of Astacus as secreting mucus for several hours. Possibly some of this time was taken up with "cleansing," which has not yet been noticed in Astacus. But if there is an actual time difference between Cambarus and Astacus it may be due to differences in temperature since Astacus lays in winter and this Cambarus in spring.

The details of the activities of a crayfish observed during the "glairing" process were in one case as follows. At first the animal kept the same unusual attitude assumed in cleansing itself, that is, it stood high up on its legs with the thorax and abdomen raised far above the bottom. The abdomen was bent forward loosely and its caudal fan reached nearly as far as the middle of the abdomen. The small limbs of the abdomen, the pleopods, swung slowly back and forth with interruptions and then, after three minutes, flapped actively back and forth. Three minutes later the crayfish gave up this attitude and crouched down and turned slightly over to one side while still swinging the pleopods and also making very active fanning movements of the exopodites of the maxillipedes. After four minutes the crayfish again stood up and swung the pleopods back and forth for five minutes and then a faint halo of glaire was first detected about the pleopods. The abdomen had now become bent forward in a curve so that it resembled a half-closed hand and the space so enclosed seemed filled with an almost invisible glaire. When the pleopods inside this mass moved there resulted a jerky movement of dirty lines where the glaire and water met at the anterior opening of the chamber formed by the bent abdomen. Two minutes later the animal ceased to stand up and lay upon its left side with all the right legs high in the water, but after lying thus for two minutes it turned onto its ventral side and crouching prone, raised its third, fourth, and fifth legs on the left side, but coming against the side of the dish, did not roll over onto its right side as was expected. By this time the long continued and increasing contractions of the muscles of the abdomen had flexed it so far forward that the tail-fan reached to the bases of the second thoracic legs, leaving only the mouthparts and the bases of the chelæ and second legs exposed to view. The pleopods were still moving rapidly back and forth inside the glaire chamber. Two minutes later, some of the legs on the right side were raised and the animal seemed about to turn over onto the left side but it returned to the ventral position. The abdomen had now become flexed even more powerfully so that its terminal piece, the telson, reached to the bases of the chelæ, or first thoracic legs, and it was pressed upward against the thorax so that some of the slightly turbid glaire was forced out from between the tail-fan and the thorax. With the abdomen thus carried forward under the thorax, the animal remained six minutes crouching down so that anteriorly the ventral side of the thorax was near the bottom of the dish while posteriorly the *dorsal* side of the abdomen rested upon the bottom. Then all the right legs were raised and the body slowly swung about through 120° till the right chela came against the end of the dish and the animal turned over onto the left side and rested with the anterior part elevated and the abdomen upon the bottom. Lying thus for some minutes the crayfish made no movements of any external organs. The tail-fan had receded a little but was still as far forward as the bases of the second thoracic legs.

Two minutes later, *i. e.*, about half an hour from the beginning of the "glairing" process, the continued recession of the abdomen laid bare the bases of the third legs and over the edge of the telson an egg was seen in the glaire above the telson. Thus the glairing period had already passed and the extrusion of eggs had been going on. A minute later the withdrawal of the abdomen stretched the glaire like a membrane from the edge of the telson to the region of the anterior thoracic legs and through this veil rows of eggs were seen issuing out from the opening of the oviduct on the base of the third right thoracic leg. The extrusion of eggs, however, will be described below from other more normal cases in which the crayfish lay upon its back and not upon one side when the eggs were extruded.

The actual extrusion of eggs was seen in six crayfish and took place in approximately the following number of minutes in these cases: 10, 10, 13, 17, 20, 30. This is in strong contrast to the statement of Chantran that, in Astacus, the extrusion of eggs lasted from one to several hours. Possibly he confounded the period of extrusion with the following period of "turning" which may well exist in Astacus and which in Cambarus occupies several hours.

In Cambarus as in Astacus it was very unusual for eggs to be laid in the day time and the above six cases were seen in the day time only from the employment of the following expedient. Crayfish that had finished the cleansing process were prevented from laying by being kept all night in running water barely sufficient to moisten them and then put into deeper water in the day time. After two or three repetitions of this treatment some ten females laid in the day time, several hours after being put into deep water.

Though no crayfish laid when merely moist, one small specimen laid in water so shallow that the animal could not cover its back when crouching down as close to the bottom as possible. This female carried on some turning movements after laying and after forty-three days the eggs, apparently all of them, hatched out, contrary to expectation.

Some individuals, however, could not be forced to lay in the day time even by numerous repetitions of the alternating conditions. Such crayfish did not lay at all, yet when examined some were found to have the ovaries full of large eggs. Others kept for two months gradually resorbed the ovarian eggs. In such ovaries the old eggs were reduced to isolated, irregular yellow masses scattered throughout the ovary, while translucent new and minute eggs filled in much of the space between the degenerated eggs.

In the cases of egg-laying observed under the above forced conditions the extrusion of eggs followed after a thorough cleansing of the region that then secreted copious glaire. By the bending of the abdomen there was then formed a chamber, or basket, full of glaire, a sort of "incubatory pouch" which received the eggs and in which they were made fast to the pleopods. The way in which the tail-fan expands to close in this pouch and the part played by the glaire, or mucus, were well described for Astacus by Lereboullet in 1860 (*Ann. Sci. Nat.*, zoöl., ser. 4, vol. 14).

Being thus provided with a basket full of glaire the female after a few trials lies down upon her back, a most remarkable position considering the energy with which such crustaceans avoid it and escape from it at other times. The flexure of the abdomen becomes so excessive that the telson is brought up as far as the bases of the chelæ, or even to half cover them, and thus the glaire is smeared over all the ventral surface of the thorax near the oviduct openings upon the bases of the third, or middle, pair of legs. The eggs will thus come out into a bag of glaire and though laid under water they are not laid into the water. The gradual relaxation of the abdomen finally uncovers the bases of the third pair of legs so that the eggs may be seen coming out of the oviducts. This withdrawal of the abdomen does not, however, expose the eggs to the water since the viscid glaire that has been put upon the thorax is drawn out from the thorax to the receding telson like an apron that covers over the eggs and prevents them from falling out even when the female turns right side up. This is the condition indicated in Fig. 5 of the preceding article in this journal.

While the eggs are emerging, the crayfish is almost motionless, lying supine with stiffly outstretched limbs and open claws as if dead. If now removed from the water and held in the hand the crayfish responds but little and the flowing out of eggs continues and may be more closely watched.

The mouths of the oviducts are widely open and remain fixed in that state when the crayfish is plunged into boiling water. It is then seen that the oval membrane that usually covers the opening is pulled outward like a curtain leaving a somewhat triangular orifice bounded on the external edge by this drawn curtain and on the median edge by the rounded rim against which the curtain comes when it is closed. Deep inside the large orifice opens the smaller oviduct tube full of eggs, each filling the tube from side to side. These eggs are also fixed by the heat in something of their natural irregular form. In life the eggs come out distorted by pressure and are so soft and flowing, like liquid in thin bags, that they mutually flatten against one another and become indented by contact with solid objects.

The eggs generally emerged in two streams one from each oviduct, but in some cases only one oviduct was used for a long time. The rate at which the eggs came out varied from 12 to 60 a minute on each side. With some stoppages and changes in speed some two to six hundred eggs were laid, by different females, in less than half an hour. Frequently the eggs came out in sets of three flattened together and the last one of the set rounded itself off during the brief pause before it was pushed away by the coming out of the next set. Thus the mouth of the oviduct was alternately taken up with one rounded egg and with three flattened eggs. When the end of deposition drew near, a gradual ending was brought about in one case by a cessation of all flow for two minutes and then the emergence of only two eggs, the last to be laid. When this animal was dissected an hour later the ovary was empty save for three eggs in the posterior lobe and two in the left oviduct and one of these slipped out of the mouth of the oviduct when the ovary was being removed. Both oviducts were greatly distended, though for a long time only the right one had been discharging eggs.

The glaire into which the eggs come is dense along the edges of the abdomen and can be picked up by forceps as ' blobs ' that hang down a half inch or so, supporting their weight. But the rest of the glaire is too weak and watery to be pulled away. When the abdomen was forcibly bent back to examine this glaire and the female prevented from laying for a night there was no second secretion of glaire over laying though cleansing movements were carried on again. When the crayfish laying eggs was suddenly put into boiling water the glaire coagulated sufficiently to form an opaque white mass over the eggs in the posterior part of the abdominal basket but the glaire over the issuing eggs did not become opaque enough to hide their red color.

The transfer of the eggs from the oviducts to the pleopods within the abdominal chamber is purely the work of gravitation. Though the crayfish lies upon its back the abdomen is always lower than the thorax and in some cases several legs were actively braced against the bottom of the dish in a manner to exaggerate this sloping of the body. In one case the animal sat propped up at an angle of nearly forty-five degrees supported upon its short fifth legs and upon the abdomen. Generally, however, only the tip of one chela and one leg touched the bottom and thus gave more stability to the animal as it lay upon its rounded back.

The deep groove between the bases of the thoracic legs favors the backward flow of the eggs which coming from each oviduct unite in one stream that flows along the thorax onto the abdomen and there divides to flow right and left along the bases of the pleopods. When, as is often the case, the animal lies with one side higher up than the other the eggs coming out of the more elevated oviduct drop some 6 to 8 mm. diagonally across the body before reaching the sternal surface. In such positions also the eggs accumulate in the lower side of the abdomen and when the animal is taken in the hand the eggs will flow right and left in the abdominal chamber as right or left is held lower. The glaire is thus not dense enough to stop the movement of eggs except at the edges of the chamber and upon the pleopods. Even after the period of extrusion and six minutes after "turning" had begun, when an undisturbed female was taken out of the water many of the eggs in the chamber ran over from side to side and tended to escape at the angle between the abdomen and the thorax on each side. Some of the eggs were then loosely attached to the pleopods, but when the abdomen was forcibly straightened out and held downward many of the eggs glided off over the end of the telson.

Though the details of action of the female at the time of extrusion of eggs were different in other cases the following special case is thought to be, in the main, typical. A crayfish lying upon its back with the telson so far forward over the thorax as to reach to the posterior edges of the second legs showed no movements of any organs for a minute and then only a slight motion of the antennules and of some legs. After four minutes more there were some slight movements of the third legs and of the left chela. The right chela rested upon the bottom of the dish and so held the animal in more stable equilibrium. By this time the slow relaxation of the abdomen had let the telson glide so far back that the bases of the third legs were nearly uncovered. Three minutes later by looking in under the telson one could see eggs coming out of the openings of both the right and the left oviducts, which openings are upon the bases of those legs.

Where the tail-fan had been over the thorax, as far forward as the chelæ, there was left a layer of glaire. On counting the eggs in the issuing streams, still three minutes later, they seemed to come out at the rate of one a second on each side. The only movements of the animal were a temporary fanning motion of an exopodite near the mouth. But five minutes later the animal had turned to lie with the left side somewhat elevated and the eggs were seen falling out of the oviduct of that side across the body then to glide back into the abdominal basket. A minute later they were coming out at the rate of ten in sixty-five seconds, in groups of two or three at one jet and then an interval before the next row of two or so. In another minute there were signs of life in the rapid fanning of exopodites on the left of the mouth, which continued for a minute, nearly stopped, and then started again. After a minute more there were added a rolling of the entire body onto an even keel and then a violent struggling of the legs as if to turn the body over into the normal prone position. Eggs were still seen in the mouths of the oviducts, two on each side. In this struggle to regain the ventral position the left side was down for a minute and then the right for a minute when the right going under and the left uppermost the animal got onto its ventral side. It then stood thus, on its legs with ventral side down, for two minutes with only slight movements of two or three legs. Immediately after this brief rest the "turning" movements began. This would no doubt have gone on for several hours but it was checked by interference after six minutes during which time there were fairly regular alternations of pose, this animal lying down first upon its left side and next upon its right.

It is in these turning movements that always follow the extrusion of eggs, that the eggs become fastened to the pleopods, so that when the female a few hours after the eggs have come out, for the first time straightens out the abdomen and the glaire is seen only as shreds hanging from the edges of the abdominal terga and from the tail-fan, the eggs do not fall into the water but henceforth hang suspended from the pleopods, till hatched.

While fastened to the pleopods the developing eggs are protected by the female and also aërated by special movements of the pleopods which are the more energetic the more the water tends to be stagnant or poor in oxygen. In all probability eggs not attached to the pleopods would never develop, in nature, and this attachment seems an essential part of the life history, here, as in many other Crustacea.

Just how the fastening of the eggs takes place is by no means clear. A microscopic examination of the so called "cement glands" upon the sterna and all the six pairs of appendages of the abdomen showed that in Cambarus, just as in Astacus, these glands contain the material from which the "glaire" is made. The same reasons that led Lereboullet (*l. c.*) and later Braun (*Arb. zoöl.-zoöt. Inst. Würzburg*, vol. 2, 1875) to believe that in Astacus this secretion fastened the eggs to the pleopods, apply in Cambarus and there is little doubt that this glaire plays the most important part in fastening the eggs. However, the remarkable fact that in both these crayfish as in crabs the eggs are fastened almost exclusively to *hairs* upon the pleopods and upon the sterna calls for explanation. In crabs Williamson (*22d Ann. Rep. Fisheries Board for Scotland,* 1904) has recently described special hairs upon the pleopods as piercing the outer egg-case and liberating an adhesive substance contained between the inner and outer part of the egg-case. His idea is that the eggs are first impaled in a row upon a hair, as upon a skewer, and subsequently fastened to the hair by the collapsing of the pierced outer egg-case and by the adhesive material contained within it. As Williamson sought to extend this view to the lobster and other Macrura, the crayfish, Cambarus, was reëxamined in April, 1905, to see if this view would apply here, but no evidence of such skewer action of hairs was found though on the other hand no *absolute* refutation of such a view was obtained.

In *Cambarus affinis* preserved eggs have in the ovary a case about $\frac{1}{3}$ $\mu$ in thickness as seen in optical section. When they leave the enveloping cellular follicle and are laid and for at least five hours afterwards, they have the same thickness of case but twenty-three hours after laying the case was (observed as above) 2 $\mu$ thick. In live eggs there is a remarkable change in elasticity accompanying this change in thickness of case. While the fresh-laid egg glides along like a liquid drop flattened and deformed by every contact and scarcely held together by its delicate case, the egg thirty-six hours afterwards is a tensely spherical ball, which, dropped nine inches onto a table, rebounds five inches and continues to bounce up and down five or six times before coming to rest. This great elasticity was noticed in Astacus eggs also, by Lereboullet. Such eggs, however, are normally hung to the pleopod by peculiar stalks. Each egg has its separate stalk and this is of elastic material comparable to the egg-case.[1] When this stalk was pulled out to four or five times its length, to ten times the diameter of the egg, it flew back like a rubber band, as soon as released.

These stalks are not formed until a little while, 15 minutes or so, after the eggs enter the abdominal chamber and at first they are exceedingly delicate, soft, wide, flat bands. These are at first very short and only slowly become as long as the diameter of the egg, subsequently to become many times that and hard and narrow and twisted. In this latter state they remain after the egg hatches and connect the empty egg-case with the pleopod and are even then a means of salvation for the young.

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[1] In a few cases an egg had two stalks with a ribbon-like connection over the surface of the egg.

Near the egg the stalk expands as a rounded tent, or bell-like membrane the edges of which are fast to the egg-case over a rounded area about one third the diameter of the egg. Optical sections indicate that the stalk continues by this membrane over the egg to make its thick elastic outer case while the thin inner case is the only one near the egg over the area covered by the bell. At this place only there seems to be a liquid separating the inner case from the walls of the bell. The stalk seems hollow for some distance up from the bell and one is led to infer that each egg is slung in a bag the closed mouth of which, when drawn out, forms the stalk. The stalk and bell look like glass, but have longitudinal creases that simulate a fibrillation. The other end of the stalk is continuous with a flat mass that binds together many of the plumose hairs along the side of the pleopod. In fact, these hairs seem rather completely invested in a secretion which holds them all imbedded in a flat mass on each side of the pleopod while from the edges of this mass hang out the egg stalks at intervals, every five or six hairs having their investment continued out as a free stalk for an egg. The stalks are like a fringe from a curtain in which the hairs are fixed; but many stalks arise from the flat sides of the curtain.

The structure of the stalk when magnified four hundred diameters is homogeneous on the outer surface but within is a clear matrix full of vesicles about $1\frac{1}{4}$ $\mu$ in diameter and elongated in the length of the stalk as if by the stretching of the matrix. When broken, in its early stages, the jagged edges of the stalk round off slightly as if somewhat paste-like.

Some facts that seem to increase the difficulty of applying Williamson's view to Cambarus are the following. One female was found in which the sterna and pleopods of the first somite were not clean and these alone had no eggs attached to their hairs so that the painfully laborious process of cleansing seems necessary for attachment of eggs, and this is more readily reconcilable with the idea that a secretion flows out over the cleansed surface to fasten the eggs than with the idea that the hairs puncture the egg-case and so liberate the material for fixation.

The "perivitelline space" which is held by Williamson to contain the adhesive material in crab's eggs seems to exist in Cambarus as the result of strong, abnormal osmotic changes only, which may accumulate liquid between the inner and the outer parts of the egg-case, when for instance an egg is plunged into strong Flemming's liquid this may accumulate in local blisters of the outer membrane.

Ovarian eggs were not sticky unless allowed to dry upon the surface when they, *either with or without the enclosing cellular follicle,* stuck to a needle and might be pulled up into club-shaped drops that then sprung up to hang as bulbs connected to the needle by a minute stalk.

The glaire, however, sticks slightly to dishes and to a knife and when eggs were taken out of the glaire from the front part of the abdominal chamber where they had not yet made stalks (though others in the back part had done so) and put into a watch glass of glaire, they stuck together more firmly than when left in water. The connection of these eggs with one another after 48 hours was by delicate fibers something like early stages of egg stalks and such eggs after fifty-eight hours were elastic so that they rebounded five or six inches when dropped nine. Thus in glaire the elastic case and something like a stalk were made when isolated from pleopods and hairs. Again, eggs broken off from very young stalks and left in moist air adhered together very firmly and also to a dead pleopod. These facts seem more readily explained by the action of the glaire than by an assumed early pricking of the hairs.

A microscopic examination of the material that binds the plumose hairs together, made some hours after the eggs were laid, showed that in some places this mass was a dense, clear, highly refracting sheet, moving and breaking under pressure like a stiff jelly, and identical with the stalks of eggs, while in other places the material on the hairs was a milky gray matrix that rounded itself off like a viscid fluid when broken and was full of droplets like those inside the cement glands. It may be that the secreted glaire passes from the latter state into the former.

The glaire itself resembles the stalks in being a clear matrix full of droplets that elongate when the glaire is stretched but while some of the droplets are $1\frac{1}{4} \times 12\frac{1}{2}$ $\mu$ others are as large as $37\frac{1}{2} \times 112$ $\mu$ and many are compound emulsive drops of 12 to 25 $\mu$. Glaire and egg-stalk are thus not identical though the stalk might well arise from glaire matrix.

Without, then, imagining any special action of the hairs we may suppose that the eggs become fastened to them because they are smeared with the densest secreted matter from the pleopod glands. All the surfaces having been made scrupulously clean the secretion can spread over the hairs as they hang like feathers in the water and as the glands along the pleopod are segmentally or interruptedly arranged, the hairs may well be stuck together in small clusters or brushes of denser glaire separated by more watery glaire. When the eggs roll down along these brushes smeared with adhesive glaire they may stick to them as the brushes stick to one another all along the side of the pleopod. Once stuck and more or less buried in the glaire on the hairs the pull of their weight will drag out enough glaire to make a stalk. That more eggs stick to the hairs than to the body of the pleopod may be largely a matter of relative area.

Some eggs that were loose in the abdominal chamber when the rest had stalks, some hours after being laid, presented the following peculiar appearance upon one side. A rounded area agreeing with the size of the bell of a stalk was thickly set with minute drops on the outside of the outer egg-case while fine threads inside this case suggested that some filose, or else secretional activity of the egg might have been going on over this area through pores in the egg-case. As was known to Chantran, each egg has a large polar area and it seems possible that special activities of the protoplasm there may be concerned in localizing the attachment of the egg to the glaire on the hairs and aid in determining the bell-like area of the stalk.

## SUMMARY

The egg-laying habits of *Cambarus affinis* are closely similar to those of Astacus, as far as the latter have been described.

In Cambarus there are four periods of activity: cleansing, glairing, extrusion, turning.

The transportation of the eggs from the oviducts to the abdominal appendages is accomplished by gravity when the female places herself in special positions.

The activities of the female include a prolonged use of special tools to cleanse the surfaces later covered by the secretions of the "cement glands," a long continued maximum contraction of the abdomen, a habit of lying supine and externally inert during oviposition, and a long rhythmic alternation of poses associated with the fastening of the eggs to the abdominal appendages. After this follow the weeks of aëration and care of the eggs till they hatch.

While the ultimate analysis of the factors concerned in fastening the eggs to the abdominal hairs awaits future investigations the secretion of the "cement glands" seems of chief importance though local activities of the egg may possibly play a part.

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